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SEXUAL SIZE DIFFERENCES IN THE GENUS *SCELOPORUS*

Henry S. Fitch

CONTENTS

ABSTRACT

Measurements were accumulated for 53 populations of *Sceloporus*, representing most of the well known species in this large, iguanid genus. Males were larger than females in 33 populations, and average male-to-female length (S-V) ratios varied from 123.9% to 87.7%. Significant trends toward females being larger than males were found in species that: a) produced a large clutch or litter (vs. small clutch or litter); b) produced a single annual clutch or litter (vs. multiple clutches or litters); c) lived in temperate (vs. tropical) climates; d) were small or medium sized (vs. large, with S-V exceeding 60 mm). Less significant correlation was found with phylogenetic groupings (Group II tending to have relatively larger males than Group III); and with mode of reproduction (viviparous species tending to have relatively larger males than oviparous species). Neither habitat (saxicolous, arboreal or terrestrial), nor development of male or female display colors, nor time of maturity (first to fourth year) showed any significant correlations with sexual size differences. Intraspecific variation in size ratios of the sexes was found in each of six polytypic species checked and in three of them (*scalaris, graciosus, occidentalis*) there was geographic shift from the male being the larger in one area to the female being the larger in another.

INTRODUCTION

In the large iguanid lizard genus *Sceloporus*, differences in size between the sexes have been noted by various authors, but no interspecific trends have been shown. In some populations males have been shown to be larger than females while in others this size relationship is reversed. In field studies of *Sceloporus occidentalis* in Oregon, *S. undulatus* in Kansas, *S. malachiticus* and *S. variabilis* in Costa Rica, and *S. jarrovi* and *S. virgatus* in Arizona, I found strikingly different size ratios between the sexes and have investigated these ratios in other species to seek possible causes and correlations for them.

Earlier (Fitch, 1976), I investigated the size relationships of the sexes in 54 mainland populations (representing 45 full species) of the iguanid genus *Anolis* and found a virtual continuum in male-to-female length ratios from 73.5% to 125.4%. Size relationships of the sexes in anoles were found to be strongly correlated with climatic conditions. Those kinds having a short and concentrated annual breeding season, enforced by unfavorably cold or dry weather prevailing for part of the year, have consistently large males, whereas those species living in aseasonal climates of rain forests and cloud forests have the sexes approximately equal in size or have females larger than males.

The *Anolis* study led to an intergeneric comparison of sexual size difference in *Sceloporus* and *Anolis*. These two successful and dominant groups of iguanid lizards often attain high population densities, generating intense competition within and between species. Both are normally territorial, with aggressive behavior and spectacular display organs well developed in males. However, *Anolis* centers its distribution in the tropics and thrives best in humid climates while *Sceloporus* centers its distribution in the warm, temperate zone and thrives best in arid climates. *Anolis* is unique among iguanids in consistently producing a one-egg clutch, laying at brief (and often regular) intervals, with left and right ovaries alternating in production. On the other hand, clutch size varies much among and within *Sceloporus* species, but with nearly always more than one egg and sometimes more than 20. In the more productive species, the capacity of the female as an egg container might be an adaptive character, subject to selection, which would alter the size relationships of the sexes. The majority of *Sceloporus* species are egg-layers, but many of those occurring in montane or northern climates are viviparous and some of the oviparous species have evolved toward viviparity by retaining their eggs until the embryos are partly developed before laying. These diverse reproductive strategies might be expected to affect the size relationships of the sexes.

The Iguanidae are one of the major families of lizards within which it is a general rule that males are larger than females. These lizards often live in open places and are visually oriented. Many kinds maintain territories and there are stereotyped species-specific display movements that serve in part as territorial signals warning away potential rivals. The display organs, often brightly colored or conspicuously marked, are different in different genera (dewlap, belly patches, underside of tail) and can be presented threateningly to potential rivals, but at most other times are either inconspicuous or are completely hidden. Species vary tremendously, both within and between genera, in size of display organ and complexity of display. The female's display organ may be rudimentary or lacking; if present it is nearly always smaller and less conspicuous than the male's. Relative size of the male in different species and genera seems to be correlated with aggressiveness and with size and conspicuousness of the display organ. Atypical iguanids include the predatory *Crotaphytus (Gam-*

belia) wislizenii in which the male is markedly smaller than the female, with no special display organ or behavior, and the solitary, cryptic, myrmecophagous *Phrynosoma* in which the sexes are approximately the same size and display organs are not developed.

METHODS AND MATERIALS

The essential data for this study were the snout-vent measurements of individual adult *Sceloporus* in substantial series. Thirty such series, from 1,973 specimens, were obtained from the collections in the University of Kansas Museum of Natural History. Measurements were available for 14 other series from published literature: Blair, 1960; Burkholder and Tanner, 1974; Cole, 1963; Crenshaw, 1955; Jackson and Telford, 1974; Mayhew, 1963; Mueller and Moore, 1969; Newlin, 1976; Parker and Pianka, 1973; Tanner and Krogh, 1973; Tinkle, 1973 and 1976; and Webb, 1967. Five series of specimens were examined in the Museum of Vertebrate Zoology, University of California collection, and four series of measurements were obtained in the course of my field studies in Kansas, Oklahoma and Costa Rica.

Whereas most of the meaurements were based on preserved museum specimens, those from my own field studies and from several published reports were taken from live lizards that were released after capture. Measurements of live material are not strictly comparable to those of preserved material. Hardening and shrinkage of the latter produced shorter measurements, perhaps several per cent less than would have been obtained from the same individuals in life. However, the length ratios of the sexes were not affected, as each series of specimens measured consisted entirely of either living or preserved animals.

The problem of setting the minimum size limits for males and females has been discussed for *Anolis* (Fitch, 1976) and is similar for *Sceloporus*. Making the state of the gonads the sole criterion would have eliminated much of the available material, collected at times other than the breeding season. Actually, the criteria were somewhat subjective. In each substantial series the distribution of records tended to approximate a normal curve, but usually was somewhat skewed, with more small adults than large adults, and relatively few in the largest size classes. This was due to the fact that size is strongly correlated with age, the largest individuals being the oldest survivors, while the smaller adults include (along with some retarded older individuals) many that are newly matured and have been exposed for a relatively short time to normal mortality factors. Obviously, the composition of any local population varies according to season, depending on the climate. Average adult size is smaller when many newly matured individuals are present and increases as these continue to grow after sexual maturity. Among the series included here are some that are composites, seasonally or geographically or both, and others that are relatively homogeneous. Some authors showing average difference between sizes of the sexes in specific populations may have used different criteria for setting lower limits for adult size. These factors would all tend to increase the variance among populations.

To account for species differences in size disparity of the sexes Wilcoxon 2-sample tests (Sokol and Rohlf, 1969) were used, with the 53 populations ranked according to their ratios and divided into two series that might be expected to differ (Table 2). Tests were somewhat limited by lack of ecological knowledge concerning the species involved. Size of clutch, frequency of clutch, time required to reach maturity, and even oviparous or viviparous habits are unknown for certain species.

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RESULTS

Range of Sexual Size Difference. TABLE 1 lists the species and populations studied, ranking them in order from the one with the highest male-to-female size ratio (*S. variabilis*) to the one with the lowest (*S. undulatus elongatus*). The ratios range from 123.9% to 87.7% in almost a continuum, but males are larger in 57% and for all series means combined, males average 104% of female length. Males are most often larger than females, being territorial, pugnacious and equipped with bright colors for display, but it is necessary to explain why the female is larger than the male in 43% of the populations and with bulk averaging as much as 1.5 times that of the male. Ten ecological traits, all interrelated, and closely linked with reproductive strategies, were statistically tested, as set forth in

TABLE 1.

POPULATION SAMPLES OF *Sceloporus* RANKED FROM HIGHEST TO LOWEST IN ORDER OF MALE-TO-FEMALE LENGTH RATIO[1]

SPECIES	♂ TO ♀ LENGTH AS PER CENT	MEAN ♂ LENGTH AND RANGE	MEAN ♀ LENGTH AND RANGE	GEOGRAPHIC ORIGIN	SOURCE
variabilis	123.95**	65.78±.46(74-57 in 97)	53.07±.491(68-44 in 157)	Costa Rica	Fitch field rec.
clarki boulengeri	123.66**	104.0±4.50(138-91 in 27)	84.1±1.58(120-72 in 36)	Sonora, Sinaloa	KU
poinsetti	120.04**	116.39±2.56(130-100 in 18)	96.95±1.80(116-86 in 21)	Chihuahua, Coahuila, Texas	KU
magister	119.50**	115.5(140-80 in 42)	96.6(120-80 in 33)	S. Calif., Ariz., N.M., Son.	Parker & Pianka 1973
pyrocephalus	117.55**	62.89±1.02(68-58 in 9)	53.50±.75(60-49 in 12)	Michoacan, Colima, Guerrero	KU
siniferus	116.24**	60.84±.456(67-53 in 32)	52.34±.42(61-48 in 35)	Oaxaca	KU
nelsoni	115.35**	60.15±.79(65-53 in 26)	52.14±.59(58-48 in 21)	Sonora, Sinaloa	KU
cozumelae	115.51**	50.72±.498(60-43 in 57)	45.484±.591(57-41 in 33)	Yucatan	KU
orcutti	110.87**	102(115-90 in 17)	92(106-85 in 77)	S. Calif.	Mayhew 1963
jarrovi	109.75**	78.75±1.53(91-61 in 35)	71.875(86-57 in 33)	Arizona	KU
insignis	108.35**	89.5(99-80 in 10)	82.6±.60(89-80 in 10)	Michoacan, Colima	Webb 1967
clarki	108.20**	102.07±1.11(118-97 in 29)	94.89±1.32(107-88 in 21)	Arizona, Sonora	KU
adleri	108.16**	65.28±1.13(72-59 in 14)	60.36±1.07(66-54 in 14)	Guerrero	KU
smaragdinus	108.00**	67.22±1.50(80-60 in 14)	62.24±1.65(77-55 in 17)	Guatemala	KU
utiformis	107.95*	64.44±1.75(75-58 in 9)	59.70±1.51(66-51 in 10)	Sinaloa, Jalisco, Nayarit	KU
magister	107.87	96 in 11	89 in 21	Utah	Tinkle 1976
teapensis	107.37**	55.87±1.03 (64-46 in 24)	52.04±.668(62-47 in 26)	Veracruz, Oaxaca, Chiapas	KU
mucronatus omiltemanus	105.43**	93.33±1.03(100-85 in 21)	88.53±1.33(100-81 in 17)	Veracruz, Guerrero	KU

TABLE 1.—(*Continued*)

Species	♂ to ♀ length as per cent	Mean ♂ length and range	Mean ♀ length and range	Geographic origin	Source
chrysostictus	105.18*	53.95±.97(62-45 in 81)	51.30±.97(61-44 in 82)	Campeche, Quintana Roo, Yucatan	KU
merriami annulatus	105.18**	47.69±.474(53-42 in 96)	45.34±.284(50-39 in 62)	Chisos Mts. Texas	KU
merriami	104.93**	52.28±.453(61-45 in 60)	49.82±.266(55-44 in 51)	S. Texas	KU
malachiticus	104.81**	79.12±.59(90-67 in 146)	75.490±.44(86-64 in 208)	Costa Rica	Fitch field records
graciosus vandenburgianus	104.70**	60.2±.44(65-55 in 34)	57.5±.47(63-51 in 26)	S. Calif.	MVZ
magister	104.59**	99.40(115-83 in 53)	95.04(107-81 in 57)	S. Nev.	Tanner & Krogh 1973
grammicus disparilis	104.02*	51.26±.540(57-42) in 23)	49.28±.498(54-44 in 32)	Coahuila, Durango	KU
occidentalis biseriatus	103.56**	75.36±.51(84-65 in 97)	72.77±.77(89-65 in 46)	S. Calif., Baja Calif.	MVZ
bulleri	103.07	100.7(116-95 in 10)	97.7(108-91 in 10)	Sinaloa to Jalisco	Webb 1967
taeniocnemis	102.81	71.11±1.11(81-65 in 19)	68.65±1.49(82-60 in 20)	Chiapas, Guatemala	KU
pictus	102.1	48.88±.443(51-47 in 8)	47.86±1.15(52-44 in 7)	Oaxaca, Puebla	KU
scalaris ("aeneus")	101.33	46.10±.709(49-42 in 10)	45.53±.621(53-41 in 23)	Michoacan, Morelos, Mexico, D.F.	KU
spinosus	101.23	88.29±1.67(99-82 in 17)	87.22±1.57(96-77 in 18)	Oaxaca	KU
torquatus	100.85	103.54±1.76(118-98 in 13)	102.67±1.46(110-97 in 9)	Jal., Mich., Mex., D.F., Guan., Agua Cal.	KU
megalepidurus	100.65	45.20±1.26(50-42 in 10)	44.91±.720(48-41 in 11)	Veracruz, Puebla	KU
undulatus consobrinus	98.94	60.31±.704(74-55 in 45)	60.96±.632(71-55 in 46)	Texas, N. Mexico	KU
graciosus	98.00	49.0 in 25	50.0 in 39	S. Utah	Tinkle 1973
formosus	96.90	71.58±1.38(80-64 in 12)	73.88±1.65(80-68 in 8)	Oaxaca	KU

TABLE 1.—(*Concluded*)

Species	♂ to ♀ length as per cent	Mean ♂ length and range	Mean ♀ length and range	Geographic origin	Source
graciosus "gracilis"	96.66**	52.1±.416(61-49 in 85	53.9±.341(63-48 in 76)	Oregon	MVZ
graciosus	95.79**	57.39(63-52 in 106)	59.91(69-53 in 121)	Utah	Burkholder and Tanner 1974
cyanogenys	95.01*	100.73±3.51(116-86 in 8)	105.91±1.44(119-88 in 22)	Texas, Tamaulipas	KU
lundelli	95.01**	90.0±1.47(93-86 in 4)	94.73±2.66(99-91 in 6)	Yucatan	KU
occidentalis occidentalis	94.0**	66.09±.694(72-61 in 23)	70.38±1.44(77-68 in 13)	W. Oregon	MVZ
woodi	94.28**	47.6	50.5	Florida	Jackson and Telford 1974
scalaris "bicanthalis"	94.14**	45.36±.63(50-43 in 14)	48.82±1.33(55-42 in 11)	Veracruz Mexico, D.F.	KU
undulatus tristichus	93.33**	58.58±.72(70-52 in 33)	62.77±.57(75-57 in 53)	Arizona N. Mexico	KU
undulatus hyacinthinus	93.13**	59.82±.59(63-57 in 18)	64.23±.87(67-57 in 11)	Oklahoma	Fitch field records
occidentalis biseriatus	93.00**	73.64±1.18(81-65 in 14)	82.73±1.43(87-72 in 21)	E. Oregon, Idaho	MVZ
undulatus garmani	92.85**	52.22±.37(59-45 in 62)	56.25±.591(68-53 in 44)	Kansas	Fitch field records
undulatus	90.33**	56.05(65-47 in 59)	62.05(70-53 in 35)	Georgia	Crenshaw 1955
undulatus erythrocheilus	89.86**	59.52±.75(65-53 in 21)	66.24±.53(72-60 in 21)	N. Mexico	KU
olivaceus	89.14**	82.9(93-60 in 34)	93.0(107-63 in 107)	Texas	Blair 1960
scalaris	88.84**	45.53±.57(55-40 in 45)	51.25±.36(60-40 in 203)	S. Calif.	Newlin 1976
virgatus	88.43**	52.0(58-48 in 11)	58.8(69-51 in 10)	S. Arizona	Fitch field records
undulatus elongatus	87.70**	63.10±1.09(71-55 in 20)	71.95±1.03(83-65 in 20)	SW Col.	KU

[1] Significant dimorphism assumed where P ≤ 0.05 (one asterisk); two asterisks indicate P ≤ 0.01.

the following sections. TABLE 2 shows the extent of correlations as revealed by Wilcoxon 2-sample tests. TABLE 3 shows the relationships of the species studied, and the occurrence of various ecological traits among them.

Phylogeny. Relationships within the genus and to other genera of iguanids are well known through many osteological, morphological, karylogical and behavioral studies (Etheridge 1964; Smith 1939; Cole 1963; Purdue and Carpenter 1972). Smith (1939) separated the 95 species and subspecies of *Sceloporus* which he considered valid into 15 groups of approximately equivalent morphological value. Smith's arrangement was accepted for 35 years, but eventually was revised and extended by Larsen and Tanner (1974 and 1975). They used over 80 characters, including lepidosis, skull morphology, distribution, behavior and karyology, and applied a statistical treatment with Ward's cluster analysis to determine degrees of relationship within the genus and construct dendrograms reflecting them. They divided the genus into three primary groups, each having several subgroups of from one to nine species. Group I, the smallest of the three, with only three subgroups and seven species, was considered to be the most primitive and the most distinct, and in the 1975 publication it was suggested to comprise a separate genus (*Lysoptychus,* Cope 1888). Group II with 20 species and Group III with 30 were each found to consist of five subgroups.

Only one species in my study, *Sceloporus (Lysoptychus) merriami* (with two populations), was a member of Group I, but 13 species of 14 populations represented all the subgroups of Group II, and 19 species with 30 populations represented all the subgroups of Group III. The samples are therefore considered to be representative of the genus, since the species not included are mostly rare and obscure ones.

In a Wilcoxon 2-sample test (Table 2), Group II and Group III are significantly different at the 95% level in sexual size differences, with Group III having relatively smaller males. However, in each group there are species in which males are larger than females, and vice versa. The subgroups show more significant contrasts. The sexes are approximately equal in size, but with males slightly larger in Group I, Subgroup B (*merriami merriami* and *merriami annulatus*) and in Group II, Subgroup A (*grammicus, pictus* and *megalepidurus*). Males are relatively large in Group II, Subgroups B (*pyrocephalus, nelsoni*), D (*siniferus, utiformis*) and E (*variabilis, cozumelae, teapensis,* and *chrysostictus*) and in Group III, Subgroups A (*spinosus coeruleopunctatus, orcutti, clarki clarki, clarki boulengeri* and *magister*—but with the notable exception of *olivaceus*) and D (*jarrovi*). Females are generally larger than males in Group III, Subgroup C (*undulatus* and subspecies, *occidentalis* except near its southern limits, *graciosus* except near its southern limits, *virgatus,* and *woodi*). In Group III, Subgroups B (*lundelli, formosus, adleri, smaragdinus, taeniocnemis,* and *malachiticus*) and D (*torquatus, cyanogenys, bulleri, insignis, mucronatus omiltemanus,* and *poinsetti*) neither sex was consistently larger.

Size of Clutch or Litter. Number of eggs per clutch varied from one (*chrysostictus*) to 19 (*torquatus*) in the specimens examined. Blair (1960) recorded a maximum of 30, laid by a large female of *olivaceus.* Mean clutch size varied from 1.8 in *cozumelae* to 14.3 in *olivaceus.* Clutch sizes of various species and populations are shown in Table 4, some based on published literature, others based on dissections of specimens in the collections of the University of Kansas Natural History Museum. Table 5 shows intraspecific variation in clutch size in the wide-ranging species *graciosus, occidentalis* and *undulatus.*

TABLE 2.

WILCOXON 2-SAMPLE TESTS OF CORRELATIONS IN *Sceloporus* POPULATIONS RANKED ACCORDING TO MALE-FEMALE LENGTH RATIOS

DIVISION OF SAMPLES	NUMBERS IN SAMPLES	t-VALUES
small brood, mean < 4	33	3.56**
vs.		
large brood, mean > 4	10	
single annual clutch or litter	28	3.36**
vs.		
multiple clutches	14	
tropical	20	2.82**
vs.		
temperate	33	
male, less than 60mm S-V	22	2.60*
vs.		
male, more than 60mm S-V	31	
Group II	14	2.23*
vs.		
Group III	37	
oviparous	36	1.97*
vs.		
viviparous	17	
saxicolous	12	1.75
vs.		
arboreal or terrestrial	35	
female display patches developed	12	1.70
vs.		
female display patches faint or absent	41	
male display patches developed	49	1.34
vs.		
male display patches faint or absent	4	
maturity attained in first year	33	.334
vs.		
maturity attained 2nd to 4th year	18	

** Significant at 99%.
* Significant at 95%.

Species whose reproductive strategy involves producing a large egg-clutch (or litter) may be subject to selective pressure to increase body size of the female as a more capacious egg container. Sexual size difference showed higher correlation with clutch size than with any other factor tested and species producing large clutches or litters tended to have relatively large females. Table 2 shows that 33 populations

TABLE 3

Ecological Traits of Various *Sceloporus* Species

Species	Single or multiple annual clutch or litter	Tropical or temperate climate	Group and subgroup	Oviparous or viviparous	Saxicolous, arboreal or terrestrial	Female display patches	Male display patches	Year of attainment of maturity
adleri	S	Trop.	III B	V	T	No	Yes	1
bulleri	S	Trop.	III E	V	S	Yes	Yes	2+
chrysostictus	M	Trop.	II E	O	T	No	No	1
clarki	M	Temp.	III A	O	A	No	Yes	1
cozumelae	M	Trop.	II E	O	T	No	No	1
cyanogenys	S	Temp.	III E	V	S	No	Yes	2+
formosus	S	Trop.	III B	V	A	No	Yes	1
graciosus	S-M	Temp.	III C	O	T	No	Yes	2
grammicus	S	Temp.	II A	V	A	No	Yes	1
insignis	S	Trop.	III E	V	S	No	Yes	2
jarrovi	S	Temp.	III D	V	S	No	Yes	1
lundelli	?	Trop.	III B	V	A	No	Yes	1
magister	S	Temp.	III A	O	A	No	Yes	2+
malachiticus	S	Trop.	III B	V	A	Yes	Yes	1
megalepidurus	S	Trop.	II A	V	?	No	No	?
merriami	S	Temp.	I B	O	S	Yes	Yes	1
mucronatus	S	Trop.	III E	V	A	No	Yes	2
nelsoni	S	Temp.	II B	O	T	No	Yes	1
occidentalis	S-M	Temp.	III C	O	A	Yes	Yes	2
olivaceus	M	Temp.	III A	O	A	No	Yes	1
orcutti	S	Temp.	III A	O	S	No	Yes	2
pictus	?	Trop.	II A	V	?	No	Yes	1
poinsetti	S	Temp.	III E	V	S	No	Yes	2+
pyrocephalus	?	Trop.	II B	O	T	No	Yes	1
scalaris	S	Temp.	II C	O-V	T	No	Yes	1
siniferus	M	Trop.	II D	O	T	No	Yes	1
smaragdinus	S	Trop.	III B	V	A	No	Yes	1
spinosus	?	Temp.	III A	O	A	No	Yes	?
taeniocnemis	S	Trop.	III B	V	A	No	Yes	1
teapensis	M	Trop.	II E	O	T	No	Yes	1
torquatus	S	Trop.	III E	V	S	No	Yes	2+
undulatus	S-M	Temp.	III C	O	S-A	Some	Yes	1-2
utiformis	M	Trop.	II D	O	T	No	No	1
variabilis	M	Trop.	II E	O	T	No	Yes	1
virgatus	S	Temp.	III C	O	T	No	No	1
woodi	M	Temp.	III C	O	T	Yes	Yes	1

TABLE 4

SIZE OF CLUTCH OR LITTER IN VARIOUS SPECIES AND POPULATIONS OF *Sceloporus*

SPECIES OR POPULATION	MEAN CLUTCH OR LITTER	RANGE	N	COUNTS FROM INDIVIDUAL FEMALES	REGION	AUTHORITY
adleri	3.8	2-6	5	2,3,4,4,6	Guerrero	KU
aeneus (=*scalaris*)	5.22±.428	4-7	9	....	Michoacan, Morelos, Mexico, D.F.	KU
bicanthalis (=*scalaris*)	6.75	....	4	....	Veracruz	KU
chrysostictus	2.43±.466	1-4	16	....	Campeche, Quintana Roo, Yucatan	KU
clarki boulengeri	8.2	....	5	4,7,10,10,10	Sinaloa	KU
cozumelae	1.8	....	12	....	Yucatan	Maslin 1963
cyanogenys	13.3	6-18	7	....	S. Texas, Tamaulipas	Hunsaker 1959
formosus	8.0	....	4	7,7,9,9	Oaxaca	KU
grammicus disparilis	5.7	4-7	7	....	Veracruz	Werler 1951
jarrovi	6.75±.32	....	52	....	S. Ariz.	Tinkle and Hadley, 1973
jarrovi	6.77	....	85	....	S. Ariz.	Goldberg 1971
jarrovi	5.37	....	52	....	S. Ariz.	Ballinger 1973
magister	6.6	4-10	7	....	S. Nev.	Tanner and Krogh, 1973
magister	8.4	3-12	14	....	S.W. states	Parker and Pianka, 1973
magister	6.2	2-9	22	....	S. Utah	Tinkle 1976
malachiticus	4.5	....	20	....	Costa Rica	Fitch 1970
merriami	3.7	2-5	27	....	S. Texas	Chaney and Gordon, 1954
mucronatus	....	....	......	9	Veracruz	Werler 1951
nelsoni	6.25	....	4	4,6,7,8	Sonora, Sinaloa	KU
olivaceus	14.3	....	......	....	Texas	Blair 1960
orcutti	11	....	......	....	S. Calif.	Mayhew 1963

TABLE 4.—(*Continued*)

Species or population	Mean clutch or litter	Range	N	Counts from individual females	Region	Authority
pictus	3.6	....	5	2,2,4,4,6	Oaxaca, Puebla	KU
poinsetti	10.45±1.01	6-23	40	....	S.W. Tex.	Ballinger 1973
pyrocephalus	4.66	....	3	3,4,7	Michoacan, Colima	KU
scalaris	6.22±0.42 1st yr ♀♀ 10.54±0.58 2nd yr and older ♀♀	....	49 37		S. Ariz.	Newlin 1976
siniferus	5.0	4-6	4	....	S. Oaxaca	KU
smaragdinus	4.20±.344	3-6	10	....	Guatemala	KU
spinosus coeruleopunctatus	12.66	8-16	6	....	Oaxaca	KU
teapensis	2.33	....	3	2,2,3	Yucatan Pen.	KU
torquatus	....	....	.....	6	Michoacan	Werler 1951
variabilis	3.0	....	18	....	Costa Rica	Fitch 1970
virgatus	9.45±2.4	4-16	184	....	S. Ariz.	Vinegar 1976
virgatus	10.2	5-15	15	....	S. Ariz.	Cole, 1963
woodi	4.13±.32	....	.....	....	Florida	Jackson and Telford, 1974

having small clutches < 4 were significantly different, at the 99% level, in sexual size difference, from 10 populations having large clutches or litters > 4.

Single or Multiple Clutches. Some species in this study are not known to produce either single clutches or multiple clutches, and are omitted. So far as I know, all viviparous species are single-brooded, since gestation extends over several months Oviparous species that are also single-brooded include *graciosus* at high elevations and northern latitudes (Burkholder and Tanner, 1974; Mueller and Moore, 1969); *merriami* (Chaney and Gordon, 1954); *virgatus* (Vinegar, 1975); *orcutti* (Mayhew, 1963); *magister* (Parker and Pianka, 1973); and *occidentalis* (Fitch, 1940; Goldberg, 1974). Species and subspecies known to be multiple brooded include *undulatus undulatus* (Crenshaw, 1955; Tinkle and Ballinger, 1972); *undulatus garmani* and *undulatus hyacinthinus* (Fitch, 1970); *woodi* (Jackson and Telford, 1974); *olivaceus* (Blair, 1960); and *variabilis* (Fitch, 1973). I found that *S. clarki boulengeri, chrysostictus, cozumelae, teapensis, spinosus coeruleopunctatus, siniferus* and *utiformis* all had young in various stages of growth at different times of year, indicating a long breeding season and multiple clutches.

The species known to be single-clutched, when arrayed against those known to have multiple clutches, and subjected to a Wilcoxon 2-sample test for correlation with sexual size difference (Ta-

TABLE 5

CLUTCH SIZE IN VARIOUS POPULATIONS OF *Sceloporus graciosus, S. occidentalis* AND *S. undulatus*

SPECIES	MEAN CLUTCH	RANGE	N	REGION	AUTHORITY
graciosus "gracilis"	3.6	......	32	Oregon, N. Calif.	Fitch, 1970
graciosus graciosus	6.03	2-10	143	N. Utah	Burkholder and Tanner, 1973
graciosus graciosus	3.8	......	72	S. Utah	Tinkle, 1973
graciosus vandenburgianus	4.24	......	25	S. Calif., Baja Calif.	Fitch, 1970
occidentalis occidentalis	7.8	......	14	W. Oregon	Fitch, 1970
occidentalis occidentalis	11.3±.41	......	......	Central Sierra, 1500 m	Jameson and Allison, 1976
occidentalis occidentalis	13.4±.57	......	......	Central Sierra, 2200 m	Jameson and Allison, 1976
occidentalis longipes	11.2	7-14	15	S. Nevada	Tanner and Hopkin, 1972
occidentalis biseriatus	7.65	3-14	37	S. Calif., Baja Calif.	Fitch, 1970
occidentalis biseriatus	7.95	......	84	Los Angeles Co., California	Goldberg, 1973
occidentalis biseriatus	7.23	......	43	Whittier, California	Goldberg, 1974
occidentalis biseriatus	8.70	......	41	San Gabriel Mts., Calif.	Goldberg, 1974
occidentalis biseriatus	8.56	......	9	E. Oregon, Idaho	Fitch unpublished (MVZ specimens)
undulatus undulatus	7.6	......	......	Georgia	Crenshaw, 1955
undulatus undulatus	7.4±.26	......	......	S. Carolina	Tinkle and Ballinger, 1972
undulatus consobrinus	6.2	3-8	13	Oklahoma	Carpenter, 1959
undulatus elongatus	6.3±.18	......	......	Utah	Tinkle, 1972
undulatus erythrocheilus	9.0	4-13	6	Oklahoma	Carpenter, 1959
undulatus garmani	7.6	5-12	10	Oklahoma	Carpenter, 1959
undulatus hyacinthinus	11.8±.47	......	......	Ohio	Tinkle and Ballinger, 1972

TABLE 6

TREND OF DECREASING MALE-TO-FEMALE SIZE FROM WARM TO COOL CLIMATE

CLIMATIC ZONE	MEAN MALE-TO-FEMALE LENGTH AS PERCENTAGE	RANGE	POPULATIONS SAMPLED N
Tropical lowlands	109.02	(93.3-130.8)	10
Tropics (both lowland and montane)	106.22	(93.3-130.8)	19
Tropical montane	103.11	(96.9-108.2)	9
Temperate zone (all samples)	100.20	(87.3-123.7)	34
Temperate (USA)	99.15	(94.3-120.1)	29
Temperate (USA excluding southern tier of states)	94.82	(87.7-107.9)	13

ble 2), showed correlation significant at the 99.9% level. The single-clutch species have relatively small males and large females.

Climate. Sceloporus occurs from about 48° 30′ N near the Canadian border in Washington south through much of the continental United States, Mexico and Central America to about 9° N in Panama. Hence, its local populations are adapted to a wide range of climates from those with long, intensely cold winters and short summers to those with hot, aseasonal climates, or those with extreme, desert conditions. Warm, dry conditions are optimum, however, since many species and individuals occur in the arid, southwestern United States and adjacent Mexico.

Seasonal schedules, and reproductive strategies obviously are much altered by climatic factors. Table 6 shows a well-defined trend from relatively small males in cooler climates to relatively large males in the hot climates of tropical lowlands. In Table 2, with 20 mainly tropical species arrayed against 33 species from temperate North America, males tend to be relatively small in the Temperate Zone, with correlation significant at the 99% level.

Body size. Adults of *Sceloporus* ranged from 39 mm S-V in female *S. merriami annulatus* to 138 in male *S. clarki boulengeri,* with means ranging from 45.2 in male *megalepidurus* to 105.9 in female *cyanogenys.* Most populations studied were in the lower size brackets with decreasing numbers toward the upper limits. The 22 smallest species (male S-V averaging less than 60 mm) when arrayed against the 31 largest (averaging more than 60 mm) were found to be significantly different (slightly below the 99% level, see Table 2). Species of small body size tend to have relatively large females. With the ten largest species (those exceeding 90 mm) arrayed against the remaining 43, difference in sexual size dimorphism was somewhat less significant ($t=1.78$).

Oviparity or Viviparity. The oviparous state, primitive for the suborder Sauria and the family Iguanidae, persists in the majority of species of *Sceloporus,* but many in montane habitats and some that are not montane have become viviparous. Still others have progressed toward viviparity by retaining eggs during part of their development.

Viviparous species include *torquatus* (Mulaik, 1946), *poinsetti* (Ballinger, 1973), *cyanogenys* (Crisp, 1964), *mucronatus omiltemanus* (Davis and Dixon, 1961), and by inference their near relatives in Group C, Subgroup E, *bulleri* and *insignis, jarrovi* (Ballinger, 1973), *malachiticus* (Fitch, 1970; Marion and Sexton, 1971) and by inference the near relatives of *malachiticus: formosus, smaragdinus, taeniocnemis* and *lundelli; aeneus* in part of its range (Thomas and Dixon, 1976), *grammicus disparilis* (Davis and Dixon, 1961; Mulaik, 1946), *pictus* (Smith and Savitsky, 1974) and *megalepidurus*. Other species are, so far as I know, oviparous.

The oviparous species, arrayed against the viviparous, show a tendency to have males smaller than females, but with the difference not significant at the 95% level (Table 2).

Habitat. The species of *Sceloporus* occur in a spectrum of habitats, terrestrial, arboreal and rocky. However, the genus is generalized, rather than highly specialized for any of these habitat types. There are some euryecic species that occur in a variety of habitats. *S. undulatus*, especially, has populations adapted to diverse habitats, including terrestrial (*garmani*), arboreal (*hyacinthinus*) and saxicolous (*elongatus*), without conspicuous morphological adaptations. In general, the terrestrial species are fine-scaled, with bodies, scales, and limbs slender and tapered, whereas arboreal and, especially, saxicolous species tend to be coarse-scaled with relatively short and thick bodies and appendages. The terrestrial species are swift runners, but scansorial species are less active and depend more on cryptic patterns and behavior and on secure hiding places in cavities and crevices.

In 22 populations considered mainly arboreal, male-to-female length ratio was most often nearly equal (mean 101.7%), with male superiority greater in 12 populations considered mainly saxicolous (mean 103.8%) and 20 populations considered mainly ground-living (mean 105.6%). None of these three groups differed statistically from the others to a significant degree. The kinds considered to be mainly saxicolous (*bulleri, cyanogenys, insignis, jarrovi, merriami, orcutti, poinsetti, torquatus* and the subspecies *elongatus* and *erythrocheilus* of *undulatus*) were most deviant from others in sexual size difference, but with difference not significant at the 95% level.

Display Patches. Brightly colored (usually deep blue) display patches are present on the chin and on the sides of the belly in the males of most species. These patches are either lacking in the female, or are barely discernible as slightly darkened areas without bright color, or if they are colorful they are paler than those of the male and less extensive in area. Even though having some display color, the female may lack either the lateral body patch or the chin patch.

Female iguanid lizards, including *Sceloporus*, are known to perform the stereotyped bobbing display of their species. Even for those that lack colorful display areas, movements may nevertheless serve for territorial assertion, or may function in species-recognition and sex-recognition.

Even within one sex in a local population, development of colored display patches may vary, being present in some, faint or absent in others, so the following groupings are somewhat arbitrary.

Females of *malachiticus, clarki, merriami* (2 populations), *bulleri, woodi, occidentalis* (3 populations) and in *undulatus* the subspecies *elongatus, erythrocheilus* and *tristichus*, have colored display patches more or less developed; in other populations female display colors are absent. In males, only *chrysostictus, cozumelae, utiformis* and *virgatus* lack bright ventral display colors. Table 2 shows that presence or absence of display colors in either sex are not strongly correlated with sexual size difference, but there seems to be some tendency for display colors to develop in females of those species where the females are relatively large.

Time Required to Mature. A combination of innate physiological traits and environmental factors affects rates of development and time required to reach maturity. This time varies in different populations, from three months to three years or more. Actual records of individuals, based on mark and recapture, are available for few populations, but well defined age-size cohorts are observable in some. In general the species are either early maturing (at age of one year or less) or late maturing (in second year or later).

The late maturing species include those of Group III, Subgroup E, *torquatus, cyanogenys* (Crisp, 1964), *poinsetti* (Ballinger, 1973) and by inference their near relatives *bulleri, insignis* and *mucronatus; graciosus* (Mueller and Moore, 1969; Tinkle, 1973), *magister* (Tanner and Krogh, 1973; Tinkle, 1976), *orcutti* (Mayhew, 1963), *occidentalis, clarki* and *undulatus,* subspecies *elongatus tristichus* and *erythrocheilus* (Fitch, 1970). So far as I know, all others are early maturing, but *megalepidurus* and *spinosus coeruleopunctatus,* being little known, were not included in the comparison. No correlation between early or late maturity and relative sizes of the sexes is indicated (Table 2).

Geographic Variation. Geographic variation in sexual size difference was found in all six species for which intraspecific comparisons were made. Seven subspecies of *Sceloporus undulatus* were tested and compared. Females were larger in all of them, but the male-to-female length ratio varied from 87.70% (*elongatus*) to 98.94% (*consobrinus*). Three populations of *S. occidentalis* were compared. In *S. occidentalis occidentalis* of western Oregon, and *S. occidentalis biseriatus* of the same latitude in eastern Oregon and Idaho, males were smaller than females—89.16% and 87.73%. However, in *S. o. biseratus* of southern California and Baja California males were slightly larger than females, 103.56%. A parallel trend was found in populations of *S. graciosus;* in northern *S. g. graciosus,* from western Oregon and northern California, Yellowstone National Park, and Utah County, Utah, males were smaller than females (96.66, 98.00 and 95.79%, respectively). However, in *S. g. vandenburgianus* of southern California, males averaged slightly larger than females (104.69%). Thus, the intraspecific trends of the wide-ranging *occidentalis* and *graciosus* in sexual size differences parallel interspecific trends for the genus as a whole.

Comparison of Species Having Small Female (variabilis) with One Having Large Female (olivaceus). Through Blair's study (1960) *S. olivaceus* of southern Texas is ecologically the best known species of *Sceloporus* by far. It is near the extreme of species having relatively large females (1.12 times male length). Most other species that have been subjects of intensive field studies, including several of the subspecies of *undulatus* (Crenshaw, 1955; Tinkle, 1972; Tinkle and Ballinger, 1972), *occidentalis* (Fitch, 1940; Tanner and Hopkin, 1972), *graciosus* (Tinkle, 1973; Tanner and Krogh, 1973; Mueller and Moore, 1969), *virgatus* (Vinegar 1975), and *woodi* (Jackson and Telford, 1974) are also among those with relatively large females, and available information suggests that, in general, their ecology and social systems are similar to those of *olivaceus.* There are no comparable studies of the species with relatively large males.

For *olivaceus,* Blair (1960) found no well-defined territories, but each adult male had a home range with a principal station and an average of 8.5 additional stations among which he distributed his time. The stations were on trees, fence posts, or other objects on which the lizards could climb. They used intervening open areas only in crossing from one station to another. Home ranges overlapped extensively and the same station might be used by two or more males, but usually both

TABLE 7

DEMOGRAPHIC TRAITS CONTRASTED IN *Sceloporus olivaceus* AND *Sceloporus variabilis*

	S. OLIVACEUS	S. VARIABILIS
Sex ratio in numbers of adults, ♂ to ♀	1 to 1.73	1 to 1.22
mean ♀ home range, m^2	275	326
mean ♂ home range, m^2	684	580
♀ to ♂ length ratio	1 to .89	1 to 1.24
♀ to hatchling length ratio	1 to .29	1 to .432
mean clutch size	14.3	3.0
number of clutches annually	3	> 3
minimum time from hatching to maturity (months)	10	4

were not present simultaneously. When two met at the same station, they fought, with one being driven off temporarily. Blair described mating as promiscuous, but his narrative account indicated that "consort pair" associations were frequent. The male might spend periods of days in close association with a temporary mate, whether or not she was sexually receptive. However, the male's range was 2.3 times that of the female's, and by shifting from one station to another he might associate with a succession of females that overlapped his range. The females were far more tolerant of one another than were the males. Often, two shared a station and Blair witnessed a female-female chase on just one occasion. In *olivaceus* the male's display patches on each side of the abdomen are small and narrow. In the female they may be absent, or when present are smaller and paler than the male's.

At the other extreme, *variabilis* is the species with greatest sexual size difference and relatively large males (1.24 times female length). Clues concerning the significance of relatively large males vs. relatively large females could no doubt be obtained by comparing ecological and behavioral data of *olivaceus* and *variabilis*. My field study of *variabilis* in Costa Rica, 1967-1970 (Fitch, 1973) did not include intensive observation of individuals, but more than 1000 lizards were individually marked and 374 were recaptured after substantial intervals. Some facts concerning the general ecology and social system of *variabilis* were obtained.

Table 7 contrasts some traits of the species *olivaceus* and *variabilis*. Significant facts revealed concerning *variabilis* are that: 1) It occurs in extremely high population densities, especially on the coast along the upper beach. In early December 1967, there were three adult males, six adult females and 52 immatures living within a 10 m radius. Four months later, in the dry season, the same area was occupied by six adult males, nine adult females and four immatures. 2) Where density is high, with ranges of many individuals including adult males, overlapping, there are not discrete territories. 3) Male display, fighting and pursuit is prominent behavior. 4) Male-female associations are common, but ephemeral. 5) The preferred habitat is seral, subject to continual successional change and to gross disturbance. On the beach, especially, favorite stations or lookouts and even the lizards themselves may be swept away in the tide and dropped at new locations (Fitch, 1973). Instability characterizes the habitat and the local population.

DISCUSSION

The relative body sizes of adult males and females in *Sceloporus* vary widely, males averaging approximately 24% longer than females at one extreme, and 12.5% shorter than females at the other extreme. In any population, the size relationship of the sexes depends on the interaction of many selective factors. The equilibrium is easily altered and even within a species local populations differ in the size ratios of the sexes.

The ecological factors that determine size ratios between the sexes in *Sceloporus* are probably somewhat different from those acting on any other group of animals. For instance, in birds and mammals and some lower vertebrates parental care of young is an important aspect of behavior, and in predatory kinds the female often protects the young against the potentially cannibalistic male. In such cases as the spotted hyena (Kruuk, 1972), and various raptorial birds (Hill, 1944; Earhart and Johnson, 1970; Mosher and Matraz, 1974) it is therefore advantageous for the female to be larger than the male. In *Sceloporus* cannibalism is rare, as these lizards are mainly insectivorous. There is no maternal care. Social behavior is primitive and does not involve family ties or group activities. A male and female may intimately associate, whether or not the female is sexually receptive. The male may habitually interact with a neighbor along a territorial boundary and he may tolerate in his territory various non-rivals, including females, juveniles and subordinate, but sexually mature, males. Presumably, any departure from parity in the sizes of the sexes permits some partitioning of food resources (Amadon, 1959; Mills, 1976; Reynolds, 1972; Selander, 1966; Verner and Willson, 1969) and the greater the size difference the smaller the overlap. Whichever sex is smaller is subject to competition from immatures. In the more prolific species, such competition might be severe at certain seasons. Larger size of the female may promote successful reproduction by relieving her of competition, both from the male and from immatures, and by permitting her to dominate the male when heterosexual competition does occur.

Compared with the diversity in anole dewlaps, the colored, ventral display areas of *Sceloporus* show remarkably little interspecific variation. The color patch on the chin, usually blue, may or may not be divided into distinct left and right portions, and may or may not be connected with the belly patches of the same color. In most species the belly patches on the two sides are separated by a paler mid-ventral area, but in old individuals of some kinds, black inner margins of the patches encroach and may fill the intervening space. In most species the dorsal color is cryptic, dull-brown or gray with streaks and spots, and with a paired series of darker transverse blotches on the back which are more prominent in juveniles and females than in adult males. In the latter, the ground color is darkened and the original markings become obscure, but when the animal is warm and active, a pale bluish or greenish area may show at the base of each scale. In the excitement of courtship or territorial defense, the colored dots expand so much that the male becomes gaudy and conspicuous and the entire body is involved in the display. Under most conditions, the belly patches are hidden as the lizard sprawls on the substrate, or raises its body only slightly in crawling and running, although the chin color may be visible from front or lateral view. However, when the lizard displays, it stands high and flattens the body in a vertical plane, puffs out the throat and turns sideways to an opponent, presenting its ventral colors conspicuously.

It might be expected that in *Sceloporus* species having relatively large males these would have: 1) well developed display patches and display behavior, 2) aggressive behavior, combat, and maintenance of well-defined territories and 3) mating systems that usually do not involve enduring pair associations, but are promiscuous or polygynous, with maintenance of leks or harems. Conversely, in species having the male smaller than the female, or near her size, he might be expected to have less prominent display, less tendency for combat and territoriality, less capacity to dominate the female, and a mating system that involes more enduring pair associations instead of harems or leks. Actually, too little is known of behavior in free-living *Sceloporus* to judge the extent of these correlations. The correlations that have been found involve traits of the female, rather than those of the male.

In mainland *Anolis*, those species living in relatively dry climates and having relatively short and concentrated breeding seasons all had males relatively large compared with females (Fitch, 1976). In contrast, those species living in relatively aseasonal climates of cloud forests or rain forests either have the sexes approximately equal in size, or have the females larger. This trend was explained by the more intense competition between males for territories and mates in the stress of a concentrated breeding season, resulting in selection for large size and aggressiveness.

Size relationships of the sexes in *Sceloporus* are not determined by the same set of factors that control them in *Anolis*. In fact, the climatic factors that generate relatively large males in *Anolis* were found to produce relatively large females in *Sceloporus*. The key to this difference seems to lie in the consistent single egg of *Anolis* versus the variable and often large clutch of *Sceloporus*. In a severely seasonal climate that limits breeding to a brief annual interval of optimum conditions, with a single clutch, there is a premium on making the clutch as large as possible. Number of eggs can be increased by making the individual eggs smaller. This has been accomplished in some instances, but, in general, the smaller the hatchling the poorer would be its chances of survival. The alternative strategy is to increase the female's capacity to produce and contain eggs by increasing her size. All the correlations with sexual size difference that were found seemed to hinge on the female's egg capacity.

There is strong support for the idea that relatively large size of the female is correlated with single broodedness, and with clutch size, in the intraspecific trends of several wide-ranging species. At the latitude of Oregon, *S. occidentalis occidentalis* and *S. o. biseriatus* which produce only one large clutch per season and require two years for the young to mature, have relatively large females (male-to-female ratio 94.0% and 93.0% respectively), but in southern California, where smaller clutches and more than one clutch are laid annually (Goldberg, 1974) with some young maturing in the first year, *biseriatus* females are relatively smaller (male-to-female ratio 103.66%). Jameson and Allison (1976) found that, in the central Sierra Nevada of California, female *occidentalis* average 2.5 mm longer at 2200 m than at 1500 m, with mean clutch size of 11.3 eggs at the lower altitude and 13.4 eggs at the higher. (They stated that the size difference between the sexes was greater at the higher altitude, but did not include figures showing male sizes.) Similarly, the small subspecies of *S. undulatus* that occur in the southern and eastern states generally produce three or more clutches annually and have males 90% or more of female length, whereas the large western subspecies, *erythrocheilus* and *elongatus*, produce only one or two clutches and have relatively smaller males (89.85 and 87.70% of female length respectively). Variation in sexual size difference is to be expected in each subspecies that occurs over a wide climatic range, altitudinally or latitudinally. In northern, single-clutched populations of *S. graciosus* females are larger than males (male-female ratio 95.79%, 96.66% and 98.0%), but in southern California the males are larger than females (104.70%) and presumably females of this population produce at least two clutches annually as Tinkle (1973) has demonstrated in those of southern Utah.

CONCLUSIONS

In 53 populations of *Sceloporus* studied, the size relationships of the sexes varied, in a virtual continuum, from relatively large males at one extreme (123.9% of female length), to relatively small males at the other extreme (87.70% of female length). Males averaged larger in 33 populations and females averaged larger in 20; for the whole group male length averaged 102.8% of female length. Sexual size difference was found to be significant at the 99% level in 42 of the 53.

The size relationships of the sexes are controlled by a complex of factors, including those of reproductive strategy, and also including social structure. Males are more aggressive than females. In most species they maintain territories by displays of colorful ventral patches and actual fighting. However, field studies of behavior under natural conditions are few and it is not yet possible to make interspecific comparisons in such traits as size and permanence of territory, permanence of association between the sexes, extent of male dominance and prevalence of polygyny. These traits are probably correlated with the relative size of the male.

The more significant correlations revealed the high female-to-male size ratio in large-brooded and single-brooded species, as contrasted with those producing small and/or multiple broods. Presumably, in the large-brooded and single-brooded species, the capacity of the female as an egg container is at a premium and there is selective pressure for her size to increase. The next strongest correlations, both above the 99% level, were those of relatively large females in temperate (as contrasted with tropical) climates and relatively large females in small or medium-sized species (as contrasted with large species, of more than 100 mm S-V). In tropical climates, breeding seasons are lengthened and reproductive effort is less concentrated than in temperate climates; the trend parallels that of multiple brooded vs. single-brooded populations. Perhaps in small species, the female's capacity as an egg container is at an even greater premium.

Weaker correlations (significant at the 95% level but not at 99%) were found between sexual size difference and the two major phylogenetic groups, and also between sexual size difference and oviparity vs. viviparity. Possible weak correlations (not significant at the 95% level) were found between sexual size difference and habitat (rock-living vs. tree- or ground-living) and between sexual size difference with large females and development of female display colors. No indication of correlation with sexual size difference was found for development of male display colors, or for time required to mature (first year vs. second to fourth year).

Intraspecific variation in sexual size difference was found in several species, notably the wide-ranging polytypic *undulatus, occidentalis* and *graciosus*. In each of these, the geographic trend paralleled that for the genus as a whole, with northern populations and those at high altitudes having relatively large females.

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